

REPORT

sPlot – A new tool for global vegetation analyses

Helge Bruelheide^{1,2,*}  | Jürgen Dengler^{2,3,4,*}  | Borja Jiménez-Alfaro^{1,2,5,*}  |
 Oliver Purschke^{1,2,*}  | Stephan M. Hennekens⁶ | Milan Chytrý⁷  | Valério
 D. Pillar⁸  | Florian Jansen⁹ | Jens Kattge^{2,10}  | Brody Sandel¹¹ | Isabelle Aubin¹² |
 Idoia Biurrun¹³  | Richard Field¹⁴  | Sylvia Haider^{1,2} | Ute Jandt^{1,2} |
 Jonathan Lenoir¹⁵  | Robert K. Peet¹⁶  | Gwendolyn Peyre¹⁷ | Francesco
 Maria Sabatini^{1,2}  | Marco Schmidt¹⁸  | Franziska Schrodtt¹⁴  | Marten Winter² |
 Svetlana Aćić¹⁹ | Emiliano Agrillo²⁰  | Miguel Alvarez²¹  | Didem Ambarlı²² |
 Pierangela Angelini²³  | Iva Apostolova²⁴ | Mohammed A. S. Arfin Khan^{25,26}  |
 Elise Arnst²⁷ | Fabio Attorre²⁰  | Christopher Baraloto^{28,29} | Michael Beckmann³⁰  |
 Christian Berg³¹ | Yves Bergeron³²  | Erwin Bergmeier³³  | Anne D. Bjorkman^{34,35} |
 Viktoria Bondareva³⁶ | Peter Borchardt³⁷ | Zoltán Botta-Dukát³⁸  | Brad Boyle³⁹ |
 Amy Breen⁴⁰ | Henry Brisse⁴¹ | Chaeho Byun⁴²  | Marcelo R. Cabido⁴³ |
 Laura Casella²³  | Luis Cayuela⁴⁴  | Tomáš Černý⁴⁵  | Victor Chepinoga⁴⁶  |
 János Csiky⁴⁷  | Michael Curran⁴⁸ | Renata Čuštrevska⁴⁹ | Zora Dajić Stevanović¹⁹ |
 Els De Bie⁵⁰  | Patrice de Ruffray⁵¹ | Michele De Sanctis²⁰  |
 Panayotis Dimopoulos⁵² | Stefan Dressler⁵³ | Rasmus Ejrnæs⁵⁴ | Mohamed Abd El-Rouf
 Mousa El-Sheikh^{55,56} | Brian Enquist³⁹ | Jörg Ewald⁵⁷ | Jaime Fagúndez⁵⁸  |
 Manfred Finckh⁵⁹ | Xavier Font⁶⁰  | Estelle Forey⁶¹  | Georgios Fotiadis⁶² |
 Itziar García-Mijangos¹³ | André Luis de Gasper⁶³  | Valentin Golub³⁶ | Alvaro
 G. Gutierrez⁶⁴  | Mohamed Z. Hatim⁶⁵ | Tianhua He⁶⁶  | Pedro Higuchi⁶⁷  |
 Dana Holubová⁷ | Norbert Hölzel⁶⁸  | Jürgen Homeier⁶⁹ | Adrian Indreica⁷⁰ |
 Deniz Işık Gürsoy⁷¹ | Steven Jansen⁷²  | John Janssen⁶ | Birgit Jedrzejek⁶⁸ |
 Martin Jiroušek^{7,73}  | Norbert Jürgens⁵⁹  | Zygmunt Kącki⁷⁴ | Ali Kavgacı⁷⁵  |
 Elizabeth Kearsley⁷⁶  | Michael Kessler⁷⁷  | Ilona Knollová⁷ | Vitaliy Kolomiychuk⁷⁸ |
 Andrey Korolyuk⁷⁹ | Maria Kozhevnikova⁸⁰ | Łukasz Kozub⁸¹ | Daniel Krstonošić⁸² |
 Hjalmar Kühl^{2,83} | Ingolf Kühn^{1,2,84}  | Anna Kuzemko⁸⁵ | Filip Kůzmič⁸⁶ |

*These authors should be considered joint first authors.

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Flavia Landucci⁷ | Michael T. Lee⁸⁷ | Aurora Levesley⁸⁸ | Ching-Feng Li⁸⁹ |
 Hongyan Liu⁹⁰ | Gabriela Lopez-Gonzalez⁸⁸ | Tatiana Lysenko^{91,92} | Armin Macanović⁹³ |
 Parastoo Mahdavi⁹⁴ | Peter Manning³⁵ | Corrado Marcenò¹³ |
 Vassiliy Martynenko⁹⁵ | Maurizio Mencuccini⁹⁶ | Vanessa Minden⁹⁷ | Jesper
 Erenskjold Moeslund⁵⁴ | Marco Moretti⁹⁸ | Jonas V. Müller⁹⁹ |
 Jérôme Munzinger¹⁰⁰ | Ülo Niinemets¹⁰¹ | Marcin Nobis¹⁰² | Jalil Noroozi¹⁰³ |
 Arkadiusz Nowak¹⁰⁴ | Viktor Onyshchenko⁸⁵ | Gerhard E. Overbeck⁸ | Wim
 A. Ozinga⁶ | Anibal Pauchard¹⁰⁵ | Hristo Pedashenko¹⁰⁶ | Josep Peñuelas^{107,108} |
 Aaron Pérez-Haase^{109,110} | Tomáš Peterka⁷ | Petr Petřík¹¹¹ | Oliver L. Phillips⁸⁸ |
 Vadim Prokhorov⁸⁰ | Valerijus Rašomavičius¹¹² | Rasmus Revermann⁵⁹ |
 John Rodwell¹¹³ | Eszter Ruprecht¹¹⁴ | Solvita Rūsiņa¹¹⁵ | Cyrus Samimi¹¹⁶ | Joop
 H.J. Schaminée⁶ | Ute Schmiedel⁵⁹ | Jozef Šibík¹¹⁷ | Urban Šilc⁸⁶ |
 Željko Škvorc⁸² | Anita Smyth¹¹⁸ | Tenekwetch Sop^{2,83} | Desislava Sopotlieva²⁴ |
 Ben Sparrow¹¹⁸ | Zvezdana Stančić¹¹⁹ | Jens-Christian Svenning³⁴ |
 Grzegorz Swacha⁷⁴ | Zhiyao Tang⁹⁰ | Ioannis Tsiripidis¹²⁰ | Pavel Dan Turtureanu¹²¹ |
 Emin Uğurlu¹²² | Domas Uogintas¹¹² | Milan Valachovič¹¹⁷ | Kim André Vanselow¹²³ |
 Yulia Vashenyak¹²⁴ | Kiril Vassilev²⁴ | Eduardo Vélez-Martin⁸ |
 Roberto Venanzoni¹²⁵ | Alexander Christian Vibrans¹²⁶ | Cyrille Violle¹²⁷ |
 Risto Virtanen^{2,128,129} | Henrik von Wehrden¹³⁰ | Viktoria Wagner¹³¹ | Donald
 A. Walker¹³² | Desalegn Wana¹³³ | Evan Weiher¹³⁴ | Karsten Wesche^{2,135,136} |
 Timothy Whitfeld¹³⁷ | Wolfgang Willner^{103,138} | Susan Wiser²⁷ |
 Thomas Wohlgemuth¹³⁹ | Sergey Yamalov¹⁴⁰ | Georg Zizka⁵³ | Andrei Zverev¹⁴¹

¹Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

³Vegetation Ecology Group, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland

⁴Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany

⁵Research Unit of Biodiversity (CSUC/UO/PA), University of Oviedo, Mieres, Spain

⁶Wageningen Environmental Research (Alterra), Wageningen University and Research, Wageningen, The Netherlands

⁷Department of Botany and Zoology, Masaryk University, Brno, Czech Republic

⁸Department of Ecology, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

⁹Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany

¹⁰Max Planck Institute for Biogeochemistry, Jena, Germany

¹¹Department of Biology, Santa Clara University, Santa Clara, California

¹²Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sault Ste Marie, Ontario, Canada

¹³Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain

¹⁴School of Geography, University of Nottingham, Nottingham, UK

¹⁵Ecologie et Dynamiques des Systèmes Anthropisés (EDYSAN, UMR 7058 CNRS-UPJV), Université de Picardie Jules Verne, Amiens, France

¹⁶Department of Biology, University of North Carolina, Chapel Hill, North Carolina

¹⁷Department of Civil and Environmental Engineering, University of the Andes, Bogota, Colombia

¹⁸Data and Modelling Centre, Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany



- ¹⁹Department of Agrobotany, Faculty of Agriculture, Belgrade-Zemun, Serbia
- ²⁰Department of Environmental Biology, "Sapienza" University of Rome, Rome, Italy
- ²¹Plant Nutrition, INRES, University of Bonn, Bonn, Germany
- ²²Department of Agricultural Biotechnology, Faculty of Agriculture and Natural Sciences, Düzce University, Düzce, Turkey
- ²³Biodiversity Conservation Department, ISPRA – Italian National Institute for Environmental Protection and Research, Rome, Italy
- ²⁴Department of Plant and Fungal Diversity and Resources, Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria
- ²⁵Forestry & Environmental Science, Shahjalal University of Science & Technology, Sylhet, Bangladesh
- ²⁶Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany
- ²⁷Manaaki Whenua–Landcare Research, Lincoln, New Zealand
- ²⁸International Center for Tropical Botany (ICTB), The Kampong of the National Tropical Botanical Garden, Coconut Grove, Florida
- ²⁹Department of Biological Sciences, Florida International University, Miami, Florida
- ³⁰Landscape Ecology, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany
- ³¹Botanical Garden, University of Graz, Graz, Austria
- ³²Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Quebec, Canada
- ³³Vegetation Ecology and Phytodiversity, University of Göttingen, Göttingen, Germany
- ³⁴Department of Bioscience, Center for Biodiversity Dynamics in a Changing World (BIOCHANGE) & Section for Ecoinformatics & Biodiversity, Aarhus University, Aarhus C, Denmark
- ³⁵Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany
- ³⁶Laboratory of Phytocoenology, Institute of Ecology of the Volga River Basin, Togliatti, Russian Federation
- ³⁷Institute of Geography, CEN – Center for Earth System Research and Sustainability, University of Hamburg, Hamburg, Germany
- ³⁸Institute of Ecology and Botany, MTA Centre for Ecological Research, Vácrátót, Hungary
- ³⁹Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona
- ⁴⁰International Arctic Research Center, University of Alaska, Fairbanks, Alaska
- ⁴¹Faculté des Sciences, MEP, Marseille Cedex 20, France
- ⁴²School of Civil and Environmental Engineering, Yonsei University, Seoul, South Korea
- ⁴³Multidisciplinary Institute for Plant Biology (IMBIV – CONICET), University of Cordoba – CONICET, Cordoba, Argentina
- ⁴⁴Department of Biology, Geology, Physics and Inorganic Chemistry, Universidad Rey Juan Carlos, Móstoles, Spain
- ⁴⁵Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Praha 6 – Suchbát, Czech Republic
- ⁴⁶Laboratory of Physical Geography and Biogeography, V.B. Sochava Institute of Geography SB RAS, Irkutsk, Russian Federation
- ⁴⁷Department of Ecology, University of Pécs, Pécs, Hungary
- ⁴⁸Institute of Environmental Engineering, Swiss Federal Institute of Technology (ETH) Zürich, Zürich, Switzerland
- ⁴⁹Institute of Biology, Faculty of Natural Sciences and Mathematics, Skopje, Republic of Macedonia
- ⁵⁰Team Biotope Diversity, Research Institute for Nature and Forest (INBO), Brussels, Belgium
- ⁵¹Institut de Biologie Moléculaire des Plantes (IBMP), Université de Strasbourg, Strasbourg, France
- ⁵²Department of Biology, Division of Plant Biology, Laboratory of Botany, University of Patras, Patras, Greece
- ⁵³Department of Botany and Molecular Evolution, Senckenberg Research Institute, Frankfurt am Main, Germany
- ⁵⁴Department of Bioscience, Aarhus University, Roende, Denmark
- ⁵⁵Botany and Microbiology Department, College of Science, King Saud University, Riyadh, Saudi Arabia
- ⁵⁶Botany Department, Faculty of Science, Damanhour University, Damanhour, Egypt
- ⁵⁷Hochschule Weihenstephan-Triesdorf, University of Applied Sciences, Freising, Germany
- ⁵⁸Faculty of Science, University of A Coruña, A Coruña, Spain
- ⁵⁹Biodiversity, Ecology and Evolution of Plants, Institute for Plant Science & Microbiology, University of Hamburg, Hamburg, Germany
- ⁶⁰Plant Biodiversity Resource Centre, University of Barcelona, Barcelona, Spain
- ⁶¹Laboratoire Ecodiv, EA 1293 URA IRSTEA, Normandie University, Mont-Saint-Aignan, France
- ⁶²Department of Forestry & Natural Environment Management, TEI of Sterea Ellada, Karpenissi, Greece
- ⁶³Department of Natural Science, Regional University of Blumenau, Blumenau, Brazil
- ⁶⁴Departamento de Ciencias Ambientales y Recursos Naturales Renovables, Facultad de Ciencias Agronomicas, Universidad de Chile, Santiago, Chile
- ⁶⁵Botany, Faculty of Science, Tanta University, Tanta, Egypt
- ⁶⁶School of Molecular and Life Sciences, Curtin University, Bentley, Australia
- ⁶⁷Forestry Department, Santa Catarina State University, Lages, Brazil
- ⁶⁸Institute of Landscape Ecology, University of Münster, Münster, Germany
- ⁶⁹Plant Ecology and Ecosystems Research, University of Göttingen, Göttingen, Germany
- ⁷⁰Department of Silviculture, Transilvania University of Brasov, Brasov, Romania



- ⁷¹Department of Biology, Celal Bayar University, Manisa, Turkey
- ⁷²Institute of Systematic Botany and Ecology, Faculty of Natural Sciences, Ulm University, Ulm, Germany
- ⁷³Department of Plant Biology, Mendel University in Brno, Brno, Czech Republic
- ⁷⁴Botanical Garden, University of Wrocław, Wrocław, Poland
- ⁷⁵Silviculture and Forest Botany, Southwest Anatolia Forest Research Institute, Antalya, Turkey
- ⁷⁶Department of Environment, Ghent University, Gent, Belgium
- ⁷⁷Department of Systematic and Evolutionary Botany, University of Zurich, Zurich, Switzerland
- ⁷⁸O.V. Fomin Botanical Garden at the Educational and Scientific Centre, Institute of Biology and Medicine, Taras Shevchenko National University of Kyiv, Kyiv, Ukraine
- ⁷⁹Geosystem Laboratory, Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences, Novosibirsk, Russian Federation
- ⁸⁰Institute of Environmental Sciences, Kazan Federal University, Kazan, Russian Federation
- ⁸¹Department of Plant Ecology and Environmental Conservation, Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Warsaw, Poland
- ⁸²Faculty of Forestry, University of Zagreb, Zagreb, Croatia
- ⁸³Primatology, Max Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig, Germany
- ⁸⁴Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle, Germany
- ⁸⁵M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine
- ⁸⁶Institute of Biology, Research Centre of Slovenian Academy of Sciences and Arts (ZRC SAZU), Ljubljana, Slovenia
- ⁸⁷NatureServe, Durham, North Carolina
- ⁸⁸School of Geography, University of Leeds, Leeds, UK
- ⁸⁹School of Forestry and Resource Conservation, National Taiwan University, Hsinchu, Taiwan
- ⁹⁰College of Urban and Environmental Sciences, Peking University, Beijing, China
- ⁹¹Department of the Phytodiversity Problems, Institute of Ecology of the Volga River Basin RAS, Togliatti, Russian Federation
- ⁹²Laboratory of Vegetation Science, Komarov Botanical Institute RAS, Saint-Petersburg, Russia
- ⁹³Department of Biology, Center for Ecology and Natural Resources – Academician Sulejman Redžić, University of Sarajevo, Sarajevo, Bosnia and Herzegovina
- ⁹⁴Research Group Vegetation Science & Nature Conservation, Department of Ecology and Environmental Science, Carl von Ossietzky-University Oldenburg, Oldenburg, Germany
- ⁹⁵Ufa Institute of Biology of Ufa Federal Scientific Centre of the Russian Academy of Sciences, Ufa, Russian Federation
- ⁹⁶Centre Research Ecology and Forestry Applications (CREAF), ICREA, Barcelona, Spain
- ⁹⁷Institute of Biology and Environmental Sciences, Carl von Ossietzky-University Oldenburg, Oldenburg, Germany
- ⁹⁸Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
- ⁹⁹Conservation Science, Royal Botanic Gardens, Kew, UK
- ¹⁰⁰AMAP – Botany and Modelling of Plant Architecture and Vegetation, IRD, CIRAD, CNRS, INRA, Université Montpellier, Montpellier, France
- ¹⁰¹Crop Science and Plant Biology, Estonian University of Life Sciences, Tartu, Estonia
- ¹⁰²Institute of Botany, Jagiellonian University, Kraków, Poland
- ¹⁰³Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria
- ¹⁰⁴Botanical Garden – Center for Biological Diversity Conservation, Polish Academy of Sciences, Warszawa, Poland
- ¹⁰⁵Laboratorio de Invasiones Biológicas (LIB), University of Concepción, Concepción, Chile
- ¹⁰⁶Amsterdam, The Netherlands
- ¹⁰⁷Global Ecology Unit CREA-FCIC-UAB, CSIC, Bellaterra, Spain
- ¹⁰⁸CREAF, Cerdanyola del Vallès, Spain
- ¹⁰⁹Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain
- ¹¹⁰Continental Ecology, Center for Advanced Studies of Blanes, Spanish Research Council (CEAB-CSIC), Blanes, Girona, Spain
- ¹¹¹Department of GIS and Remote Sensing, Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic
- ¹¹²Institute of Botany, Nature Research Centre, Vilnius, Lithuania
- ¹¹³Lancaster, UK
- ¹¹⁴Hungarian Department of Biology and Ecology, Faculty of Biology and Geology, Babeş-Bolyai University, Cluj-Napoca, Romania
- ¹¹⁵Department of Geography, University of Latvia, Riga, Latvia
- ¹¹⁶Climatology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany
- ¹¹⁷Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Bratislava, Slovakia
- ¹¹⁸TERN, University of Adelaide, Adelaide, Australia
- ¹¹⁹Faculty of Geotechnical Engineering, University of Zagreb, Varaždin, Croatia
- ¹²⁰School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece



- ¹²¹A. Borza Botanical Garden, Babeş-Bolyai University, Cluj-Napoca, Romania
- ¹²²Forest Engineering Department, Faculty of Forestry, Bursa Technical University, Yıldırım, Bursa, Turkey
- ¹²³Department of Geography, University of Erlangen-Nuremberg, Erlangen, Germany
- ¹²⁴Khmelnitskyi Institute of Interregional Academy of Personnel Management, Khmelnytskyi, Ukraine
- ¹²⁵Department of Chemistry, Biology and Biotechnology, University of Perugia, Perugia, Italy
- ¹²⁶Departamento de Engenharia Florestal, Universidade Regional de Blumenau, Blumenau, Brazil
- ¹²⁷Centre d'Ecologie Fonctionnelle et Evolutive (UMR5175), CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, Montpellier, France
- ¹²⁸Ecology and Genetics Research Unit, Biodiversity Unit, University of Oulu, Oulu, Finland
- ¹²⁹Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Leipzig, Germany
- ¹³⁰Institute of Ecology, Leuphana University, Lüneburg, Germany
- ¹³¹Department of Biological Sciences, University of Alberta, Edmonton, Canada
- ¹³²Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska
- ¹³³Department of Geography & Environmental Studies, Addis Ababa University, Addis Ababa, Ethiopia
- ¹³⁴Department of Biology, University of Wisconsin – Eau Claire, Eau Claire, Wisconsin
- ¹³⁵Botany Department, Senckenberg Museum of Natural History Görlitz, Görlitz, Germany
- ¹³⁶International Institute Zittau, Technical University Dresden, Zittau, Germany
- ¹³⁷Department of Ecology and Evolutionary Biology/Brown University Herbarium, Brown University, Providence, Rhode Island
- ¹³⁸Vienna Institute for Nature Conservation & Analyses, Vienna, Austria
- ¹³⁹Research Unit Forest Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland
- ¹⁴⁰Laboratory of Wild-Growing Flora, Botanical Garden-Institute, Ufa Scientific Centre, Russian Academy of Sciences, Ufa, Russian Federation
- ¹⁴¹Department of Botany, Tomsk State University, Tomsk, Russian Federation

Correspondence

Helge Bruelheide, Institute of Biology/
Geobotany and Botanical Garden, Martin
Luther University Halle-Wittenberg, Halle,
Germany.
Email: helge.bruehlheide@botanik.uni-halle.de

Co-ordinating Editor: Alessandro Chiarucci

Abstract

Aims: Vegetation-plot records provide information on the presence and cover or abundance of plants co-occurring in the same community. Vegetation-plot data are spread across research groups, environmental agencies and biodiversity research centers and, thus, are rarely accessible at continental or global scales. Here we present the sPlot database, which collates vegetation plots worldwide to allow for the exploration of global patterns in taxonomic, functional and phylogenetic diversity at the plant community level.

Results: sPlot version 2.1 contains records from 1,121,244 vegetation plots, which comprise 23,586,216 records of plant species and their relative cover or abundance in plots collected worldwide between 1885 and 2015. We complemented the information for each plot by retrieving climate and soil conditions and the biogeographic context (e.g., biomes) from external sources, and by calculating community-weighted means and variances of traits using gap-filled data from the global plant trait database TRY. Moreover, we created a phylogenetic tree for 50,167 out of the 54,519 species identified in the plots. We present the first maps of global patterns of community richness and community-weighted means of key traits.

Conclusions: The availability of vegetation plot data in sPlot offers new avenues for vegetation analysis at the global scale.

KEYWORDS

biodiversity, community ecology, ecoinformatics, functional diversity, global scale, macroecology, phylogenetic diversity, plot database, sPlot, taxonomic diversity, vascular plant, vegetation relevé

1 | INTRODUCTION

Studying global biodiversity patterns is at the core of macroecological research (Costello, Wilson, & Houlding, 2012; Kreft & Jetz, 2007; Wiens, 2011), since their exploration may provide insights into the ecological and evolutionary processes acting at different spatio-temporal scales (Ricklefs, 2004). The opportunities engendered by the compilation of large collections of biodiversity data into widely accessible global (GBIF, www.gbif.org) or continental databases (e.g., BIEN, www.bien.nceas.ucsb.edu/bien) have recently advanced our understanding of global biodiversity patterns, especially for vertebrates, but also for vascular plants (Butler et al., 2017; Engemann et al., 2016; Lamanna et al., 2014; Swenson et al., 2012). Although this development has led to the formulation of several macroecological theories (Currie et al., 2004; Pärtel, Bennett, & Zobel, 2016), a more mechanistic understanding of how assembly processes shape ecological communities, and consequently global biodiversity patterns, is still missing (Lessard, Belmaker, Myers, Chase, & Rahbek, 2012).

Understanding the links between biodiversity patterns and assembly processes requires fine-grain data on the co-occurrence of species in ecological communities, sampled across continental or global spatial extents (Beck et al., 2012; Wisz et al., 2013). For example, such co-occurrence data have been used to compare changes in vegetation composition over time spans of decades (Jandt, von Wehrden, & Bruelheide, 2011; Perring et al., 2018). Unfortunately, up to now information on fine-grain vegetation data has not been readily available, as most of the continental to global biodiversity

datasets have been derived from occurrence data (i.e., presence-only data), and after being aggregated spatially, have a relatively coarse-grain scale (e.g., one-degree grid cells) without information on species co-occurrence at the meaningful scale of local communities (Boakes et al., 2010). In contrast, vegetation-plot data record the cover or abundance of each plant species that occurs in a plot of a given size at the date of the survey, representing the main reservoir of plant community data worldwide (Dengler et al., 2011).

Vegetation-plot data differ in fundamental ways from databases of occurrence records of individual species aggregated at the level of grid cells or regions of hundreds or thousands of square kilometers (Figure 1). First, vegetation plots usually provide information on the relative cover or relative abundance of species, allowing for the testing of central theories of biogeography, such as the abundance-range size relationship (Gaston & Curnutt, 1998) or the relationship between local abundance and niche breadth (Gaston et al., 2000). Second, they contain information on which plant species co-occur in the same locality (Chytrý et al., 2016), which is a necessary precondition for direct biotic interactions among plant individuals. Third, unrecorded species can be considered truly absent from the aboveground vegetation at this scale because the standardized methodology of taking a vegetation record requires a systematic search for all species in a plot, or at least all species of the dominant functional group. Fourth, many plots are spatially explicit and can be resurveyed through time to assess possible consequences of land use and climate change (Perring et al., 2018; Steinbauer et al., 2018). Fifth, vegetation plots represent a snapshot of the primary producers of a terrestrial ecosystem, which can be functionally linked to

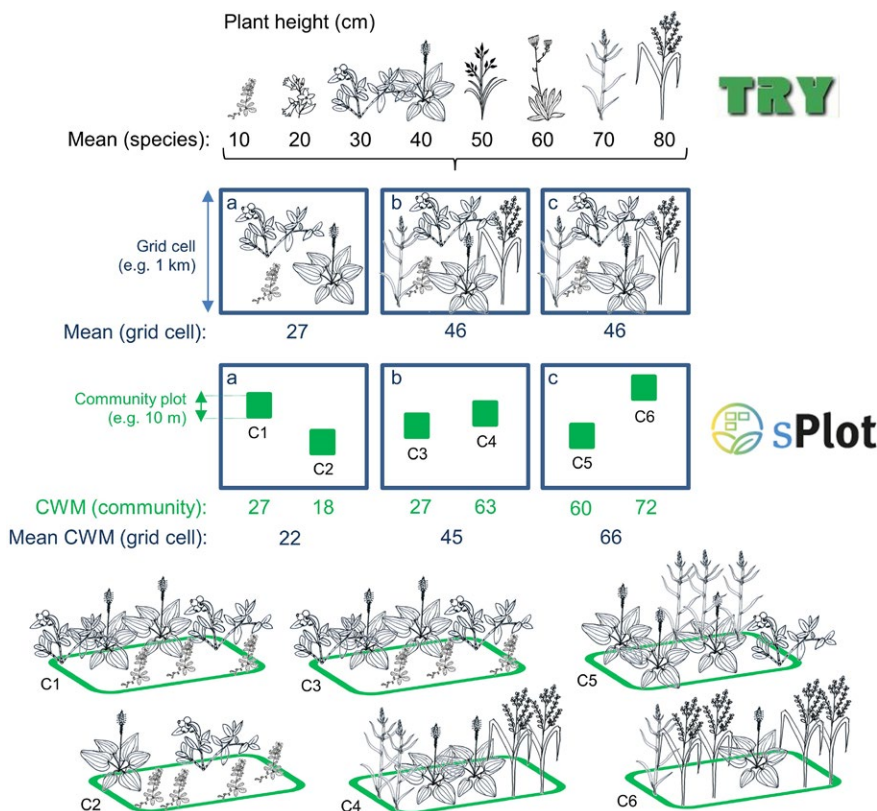


FIGURE 1 Conceptual figure visualizing how functional composition (in this case plant height) differs between calculations based on mean traits for grid cells and community data sampled in vegetation plots. Occurrence data (e.g., from distribution atlases, GBIF, etc.) can be used to calculate mean trait values in grid cells G1–G3. However, community weighted means (CWMs) of traits differ across local plots (P1–P6), while the mean values of CWMs in the grid cells differ from the unweighted values calculated in the grid cells. This example is simplified by showing few species and few plots. In reality, differences are generally more pronounced



organisms from different trophic groups sampled in the same plots (e.g., multiple-taxa surveys) and related processes and services both below (e.g., decomposition, nutrient cycling) and above ground (e.g., herbivory, pollination) (e.g., Schuldt et al., 2018).

Recently several projects at the regional to continental scale have demonstrated the potential of using vegetation-plot databases for exploring biodiversity patterns and the underlying assembly processes. Using vegetation data of French grasslands, Borgy et al. (2017) demonstrated that weighting leaf traits by species abundance in local communities is pivotal to capture leaf trait–environment relationships. Analyzing United States forest assemblages surveyed at the community level, Šímová, Rueda, and Hawkins (2017) were able to relate cold or drought tolerance to leaf traits, dispersal traits and traits related to stem hydraulics. Using plot-based tree inventories of the United States forest service, Zhang, Niinemets, Sheffield, and Lichstein (2018) found that shifts in tree functional composition amplify the response of forest biomass to droughts. Based on >15,000 plots from a wide number of habitat types in Denmark, Moeslund et al. (2017) showed that typical plant species that are part of the site-specific species pool but are absent in a community tend to depend on mycorrhiza, are mostly adapted to low light and low nutrient levels, have poor dispersal abilities and are ruderals and stress-intolerant. By collating >40,000 vegetation plots sampled in European beech forests, Jiménez-Alfaro et al. (2018) found that current local community diversity and species pool sizes calculated at different scales were mainly explained by proximity to glacial refugia and current precipitation.

Although large collections of vegetation-plot data are now available from national to continental levels (e.g., Chytrý et al., 2016; Enquist, Condit, Peet, Schildhauer, & Thiers, 2016; Peet, Lee, Jennings, & Faber-Langendoen, 2012; Schaminée, Hennekens, Chytrý, & Rodwell, 2009; Schmidt et al., 2012), they are rarely used

in global-scale biodiversity research (Franklin, Serra-Diaz, Syphard, & Regan, 2017; Wiser, 2016). This is unfortunate because vegetation-plot data may reveal important patterns that cannot be captured by grid-based datasets (Table 1). Functional composition patterns, for instance, may differ substantially when considering vegetation-plot data rather than single species occurrences aggregated at the level of coarse-grain grid cells. Using plant height as an illustration reveals that the trait means calculated on all the species occurring in a grid cell may differ strongly from the community-weighted means (CWMs) averaged across local communities (Figure 1). Nevertheless, only the grid-based approach has been used to date in studies of the geographic distribution of trait values (e.g., Swenson et al., 2012, 2017; Wright et al., 2017).

Here, we present sPlot, a global database for compiling and integrating plant community data. We describe (a) main steps in integrating vegetation-plot data in a repository that provides taxonomic, functional and phylogenetic information on co-occurring plant species and links it to global environmental drivers; (b) principal sources and properties of the data and the procedure for data usage; and (c) expected impacts of the database in future ecological research. To illustrate the potential of sPlot we also show global diversity patterns that can be readily derived from the current content.

2 | COMPILATION OF THE SPLOT DATABASE

2.1 | Vegetation-plot data

The sPlot consortium currently collates 110 vegetation-plot databases of regional, national or continental extent. Some of the databases have previously been aggregated by and contributed through

TABLE 1 Types of information provided by single vegetation plots, vegetation plots aggregated within grid cells (or other geographic units) and single species occurrence records aggregated within grid cells. The three levels are illustrated in Figure 1

| Information from... | Single vegetation plots | Set of vegetation plots aggregated within grid cells | Grid-cell data from floristic inventories |
|----------------------------------|--|---|--|
| To derive information on the ... | Plot level | Grid cell level | Grid cell level |
| Type of occurrence | Co-occurrence, occurrence by vegetation type | Occurrence by vegetation type | Occurrence |
| Community assembly rules | Yes (co-occurrence is a prerequisite for species interactions) | No | No |
| Absences | Yes (for the target plant group in a study) | No (except for intensive sampling schemes) | Depending on sampling intensity |
| Floristic composition | ... of the local community | ... of the species pools of vegetation types | ... of the total set of species |
| Diversity | α | β , γ | γ |
| Species abundance | Local cover-abundance | Mean cover-abundance and frequency by vegetation type | Occurrence only |
| Combination with traits | Functional composition of the local community (traits unweighted or weighted by cover: CWM, CWV) | Functional composition of the species pool (unweighted or weighted) | Functional composition of the total set of species (unweighted only) |
| Environmental filtering | ... at the local level | ... at the regional level | ... at the regional level |



two (sub-)continental database initiatives (Table 2 and Appendix S1). All data from Europe and nearby regions were contributed via the European Vegetation Archive (EVA), using the SynBioSys taxon database as a standard taxonomic backbone (Chytrý et al., 2016). Three African databases were contributed via the Tropical African Vegetation Archive (TAVA). In addition, multiple U.S. databases were contributed through the VegBank archive maintained in support of the U.S. National Vegetation Classification (Peet, Lee, Boyle, et al., 2012; Peet, Lee, Jennings, & Faber-Langendoen, 2012). The data from other regions (South America, Asia) were contributed as separate databases.

We stored the vegetation-plot data from the individual databases in the database software TURBOVEG v2 (Hennekens & Schaminée, 2001). Our general procedure was to preserve the original structure and content of the databases as much as possible in order to facilitate regular updates through automated workflows. The individual databases were then integrated into a single SQLite database using TURBOVEG v3 (S.M. Hennekens, ALTErra, The Netherlands; www.synbiosys.alterra.nl/turboveg3/help/en/index.html). TURBOVEG v3 combines the species lists from the original databases in a single repository and links the plot attributes (so-called header data) to 58 descriptors of vegetation-plots (Table S2.1 in Appendix S2). The metadata of the databases collated in sPlot were managed through the Global Index of Vegetation-Plot Databases (GIVD; Dengler et al., 2011), using the GIVD ID as the identifier. The current sPlot version 2.1 was created in October 2016 and contains 1,121,244 vegetation plots with 23,586,216 plant species \times plot observations (i.e., records of a species in a plot). Most records (1,073,737; 95.8%) have information on cover, 29,288 on presence/absence, 5,854 on basal area, 4,883 on number of stems (often in addition to basal area), 148 on importance value (a combination of basal area and number of stems), 3,265 on counts of individuals, 1,895 on percentage frequency, and further 2,174 have a mix of these different types of metrics.

2.2 | Taxonomic standardization

To combine the species lists of the different databases in sPlot, we constructed a taxonomic backbone. To link co-occurrence information in sPlot with plant traits, we expanded this backbone to integrate plant names used in the TRY database (Kattge et al., 2011). The taxon names (without nomenclatural authors) from sPlot 2.1 and TRY 3.0 were first concatenated into one list, resulting in 121,861 names, of which 61,588 (50.5%) were unique to sPlot; 35,429 (29.1%) unique to TRY; and 24,844 (20.4%) shared between TRY and sPlot. Taxon names were parsed and resolved using the Taxonomic Name Resolution Service web application (TNRS version 4.0; Boyle et al., 2013; iPlant Collaborative, 2015), using the five TNRS standard sources ranked by default. We allowed for (a) partial matching to the next higher rank (genus or family) if the full taxon name could not be found and (b) full fuzzy matching, to return names that were matched within a maximum number of four single-character edits (Levenshtein edit distance of 4), which corresponds to the minimum match accuracy of 0.05 in TNRS, with 1 indicating a perfect match.

We accepted all names that were matched, or converted from synonyms, with an overall match score of 1. In cases with no exact match (i.e., the overall match score was <1), names were inspected on an individual basis. All names that matched at taxonomic ranks at or lower than species (e.g., subspecies, varieties) were accepted as correct names. The name matching procedure was repeated for the uncertain names (i.e., with match accuracy scores below the threshold value from the first matching run), with a preference on first using the source 'Tropicos' (Missouri Botanical Garden; <http://www.tropicos.org/>; accessed 19 Dec 2014) because here matching scores were often higher for names of low taxonomic rank. The remaining 9,641 non-matched names were resolved using (a) the additional source 'NCBI' (Federhen, 2010) within TNRS, (b) the matching tools in the Plant List web application (The Plant List 2013), (c) the 'tpl'-function within the R-package 'Taxonstand' (Cayuela, Stein, & Oksanen, 2017) and (d) manual inspection (i.e., to resolve vernacular names). All subspecies were aggregated to the species level. Names that could not be matched were classified as 'No suitable matches found'. Because sPlot and TRY contain taxa of non-vascular plants, we tagged vascular plant names based on their family and phylum affiliation, using the 'rgbif' library in R (Chamberlain, 2017). Of the full list of plant names in sPlot and TRY, 79,171 (94.6%) plant names were matched at the species level, 4,343 (5.2%) at the genus level, 152 (0.2%) at the family level and 13 names at higher taxonomic levels. Overall, this led to 58,066 accepted taxon names in sPlot. Family affiliation was classified according to APG III (APG III, 2009). A detailed description of the workflow, including R-code, is available in Purschke (2017a).

One potential shortcoming of our taxonomic backbone is that for most regions it was necessary to standardize taxa using standard sets of taxonomic synonyms. Thus, if a taxonomic name represents multiple taxonomic concepts, e.g., such as created by the splitting and lumping of taxa, or a name has been misapplied in a region, we must trust that this problem has been addressed in our component databases (Franz, Peet, & Weakley, 2004; Jansen & Dengler, 2010). However, different component databases may have applied different taxonomic concepts for splitting and lumping taxa.

2.3 | Physiognomic information

To achieve a classification into forests versus non-forests that is applicable to all plots irrespective of the structural and habitat data provided by the source database, we defined as forest all plot records that had $>25\%$ absolute cover of the tree layer, making use of the attribute data of sPlot. This threshold is similar to the classification of Ellenberg and Müller-Dombois (1967), who defined woodland formations with trees covering more than 30%. There were 16,244 tree species in the sPlot database. As tree layer cover was available for only 25% of all plots, we additionally used the information whether the taxa present in a plot were trees (usually defined as being taller than 5 m), using the plant growth form information from TRY (see below). Thus, plots lacking tree cover information were defined as forests if the sum of relative cover of all tree taxa was

**TABLE 2** Plot datasets included in sPlot 2.1

| GIVD ID | Database name | # of plots in sPlot 2.1 | Custodian | Deputy custodian | Reference |
|--------------|---|-------------------------|---------------------|-------------------------|---|
| [Aggregator] | European Vegetation Archive (EVA) | 950,001 | Milan Chytrý | Ilona Knollová | Chytrý et al. (2016) |
| 00-00-004 | Vegetation Database of Eurasian Tundra | 1,132 | Risto Virtanen | | |
| 00-RU-001 | Vegetation Database Forest of Southern Ural | 1,102 | Vassiliy Martynenko | | |
| 00-RU-003 | Database Meadows and Steppes of Southern Ural | 2,354 | Sergey Yamalov | Mariya Lebedeva | |
| 00-TR-001 | Forest Vegetation Database of Turkey - FVDT | 919 | Ali Kavgacı | | |
| 00-TR-002* | Non-forest Vegetation Database of Turkey | 3,018 | Deniz Işık Gürsoy | Didem Ambarlı | |
| AS-TR-002 | Vegetation Database of Oak Communities in Turkey | 1,181 | Emin Uğurlu | | |
| EU-00-002 | Nordic-Baltic Grassland Vegetation Database (NBGVd) | 7,675 | Jürgen Dengler | Łukasz Kozub | Dengler and Růsina (2012) |
| EU-00-011 | Vegetation-Plot Database of the University of the Basque Country (BIOVEG) | 18,441 | Idoia Biurrun | Itziar García-Mijangos | Biurrun, García-Mijangos, Campos, Herrera, and Loidi (2012) |
| EU-00-013 | Balkan Dry Grasslands Database | 7,683 | Kiril Vassilev | Armin Macanović | Vassilev, Dajič, Čuštrevska, Bergmeier, and Apostolova (2012) |
| EU-00-016 | Mediterranean Ammophiletea Database | 7,359 | Corrado Marcenò | Borja Jiménez-Alfaro | Marcenò and Jiménez-Alfaro (2017) |
| EU-00-017 | European Coastal Vegetation Database | 4,624 | John Janssen | | |
| EU-00-018 | The Nordic Vegetation Database | 5,477 | Jonathan Lenoir | Jens-Christian Svenning | Lenoir et al. (2013) |
| EU-00-019 | Balkan Vegetation Database | 9,118 | Kiril Vassilev | Hristo Pedashenko | Vassilev et al. (2016) |
| EU-00-020 | WetVegEurope | 14,111 | Flavia Landucci | | Landucci et al. (2015) |
| EU-00-022 | European Mire Vegetation Database | 10,147 | Tomáš Peterka | Martin Jiroušek | Peterka, Jiroušek, Hájek, and Jiménez-Alfaro (2015) |
| EU-AL-001 | Vegetation Database of Albania | 290 | Michele De Sanctis | Giuliano Fanelli | De Sanctis, Fanelli, Mullaj, and Attorre (2017) |
| EU-AT-001 | Austrian Vegetation Database | 34,458 | Wolfgang Willner | Christian Berg | Willner, Berg, and Heiselmayer (2012) |
| EU-BE-002 | INBOVEG | 25,665 | Els De Bie | | |
| EU-BG-001 | Bulgarian Vegetation Database | 5,254 | Iva Apostolova | Desislava Sopotlieva | Apostolova, Sopotlieva, Pedashenko, Velev, and Vasilev (2012) |
| EU-CH-005 | Swiss Forest Vegetation Database | 14,193 | Thomas Wohlgemuth | | Wohlgemuth (2012) |
| EU-CZ-001 | Czech National Phytosociological Database | 104,697 | Milan Chytrý | Dana Holubová | Chytrý and Rafajová (2003) |

(Continues)

**TABLE 2** (Continued)

| GIVD ID | Database name | # of plots in sPlot 2.1 | Custodian | Deputy custodian | Reference |
|-----------|---|-------------------------|----------------------------|-----------------------|--|
| EU-DE-001 | VegMV | 53,822 | Florian Jansen | Christian Berg | Jansen, Dengler, and Berg (2012) |
| EU-DE-013 | VegetWeb Germany | 23,078 | Jörg Ewald | | Ewald, May, and Kleikamp (2012) |
| EU-DE-014 | German Vegetation Reference Database (GVRD) | 30,840 | Ute Jandt | Helge Bruelheide | Jandt and Bruelheide (2012) |
| EU-DK-002 | National Vegetation Database of Denmark | 24,264 | Jesper Erenskjold Moeslund | Rasmus Ejrnæs | |
| EU-ES-001 | Iberian and Macaronesian Vegetation Information System (SIVIM)-Wetlands | 6,560 | Aaron Pérez-Haase | Xavier Font | |
| EU-FR-003 | SOPHY | 209,864 | Henry Brisse | Patrice de Ruffray | Brisse, de Ruffray, Grandjouan, and Hoff (1995) |
| EU-GB-001 | UK National Vegetation Classification Database | 28,533 | John S. Rodwell | | |
| EU-GR-001 | KRITI | 292 | Erwin Bergmeier | | |
| EU-GR-005 | Hellenic Natura 2000 Vegetation Database (HelNatVeg) | 5,168 | Panayotis Dimopoulos | Ioannis Tsiripidis | Dimopoulos and Tsiripidis (2012) |
| EU-GR-006 | Hellenic Woodland Database | 3,199 | Georgios Fotiadis | Ioannis Tsiripidis | Fotiadis, Tsiripidis, Bergmeier, and Dimopoulos (2012) |
| EU-HR-001 | Phytosociological Database of Non-Forest Vegetation in Croatia | 5,057 | Zvezdana Stančić | | Stanić (2012) |
| EU-HR-002 | Croatian Vegetation Database | 8,734 | Željko Škvorc | Daniel Krstonošić | |
| EU-HU-003 | CoenoDat Hungarian Phytosociological Database | 8,505 | János Csiky | Zoltán Botta-Dukát | Lájer et al. (2008) |
| EU-IT-001 | VegItaly | 15,332 | Roberto Venzoni | Flavia Landucci | Landucci et al. (2012) |
| EU-IT-010 | Italian National Vegetation Database (BVN/ISPRA) | 3,562 | Laura Casella | Pierangela Angelini | Casella, Bianco, Angelini, and Morroni (2012) |
| EU-IT-011 | Vegetation-Plot Database Sapienza University of Rome (VPD-Sapienza) | 12,780 | Emiliano Agrillo | Fabio Attorre | Agrillo et al. (2017) |
| EU-LT-001 | Lithuanian Vegetation Database | 7,821 | Valerijus Rašomavičius | Domas Uogintas | |
| EU-LV-001 | Semi-natural Grassland Vegetation Database of Latvia | 5,594 | Solvita Rūsiņa | | Rūsiņa (2012) |
| EU-MK-001 | Vegetation Database of the Republic of Macedonia | 1,417 | Renata Ćušterevska | | |
| EU-NL-001 | Dutch National Vegetation Database | 102,327 | Joop H.J. Schaminée | Stephan M. Hennekens | Schaminée et al. (2006) |
| EU-PL-001 | Polish Vegetation Database | 22,229 | Zygmunt Kącki | Grzegorz Swacha | Kącki and Śliwiński (2012) |
| EU-RO-007 | Romanian Forest Database | 6,017 | Adrian Indreica | Pavel Dan Turtureanu | Indreica, Turtureanu, Szabó, and Irimia (2017) |
| EU-RO-008 | Romanian Grassland Database | 1,921 | Eszter Ruprecht | Kiril Vassilev | Vassilev et al. (2018) |
| EU-RS-002 | Vegetation Database Grassland Vegetation of Serbia | 5,587 | Svetlana Aćić | Zora Dajić Stevanović | Aćić, Petrović, Šilc, and Dajić Stevanović (2012) |

(Continues)



TABLE 2 (Continued)

| GIVD ID | Database name | # of plots in sPlot 2.1 | Custodian | Deputy custodian | Reference |
|--------------|--|-------------------------|----------------------|------------------------|---|
| EU-RU-002 | Lower Volga Valley Phytosociological Database | 14,853 | Valentin Golub | Viktoria Bondareva | Golub et al. (2012) |
| EU-RU-003 | Vegetation Database of the Volga and the Ural Rivers Basins | 1,516 | Tatiana Lysenko | | Lysenko, Mitroshenkova, and Kalmykova (2012) |
| EU-RU-011 | Vegetation Database of Tatarstan | 7,471 | Vadim Prokhorov | Maria Kozhevnikova | Prokhorov, Rogova, and Kozhevnikova (2017) |
| EU-SI-001 | Vegetation Database of Slovenia | 10,986 | Urban Šilc | Filip Kuzmič | Šilc (2012) |
| EU-SK-001 | Slovak Vegetation Database | 36,405 | Milan Valachovič | Jozef Šibík | Šibík (2012) |
| EU-UA-001 | Ukrainian Grasslands Database | 4,043 | Anna Kuzemko | Yulia Vashenyak | Kuzemko (2012) |
| EU-UA-006 | Vegetation Database of Ukraine and Adjacent Parts of Russia | 3,326 | Viktor Onyshchenko | Vitaliy Kolomiychuk | |
| [Aggregator] | Tropical African Vegetation Archive (TAVA) | 6,677 | Marco Schmidt | Stefan Dressler | Janßen et al. (2011) |
| AF-00-001 | West African Vegetation Database | 3,129 | Marco Schmidt | Georg Zizka | Schmidt et al. (2012) |
| AF-00-008 | PANAF Vegetation Database | 2,469 | Hjalmar Kühl | TeneKwetché Sop | |
| AF-BF-001 | Sahel Vegetation Database | 1,079 | Jonas V. Müller | Marco Schmidt | Müller (2003) |
| | Other databases | 164,566 | | | |
| 00-00-001 | RAINFOR data managed by ForestPlots.net | 1,827 | Oliver L. Phillips | Aurora Levesley | Lopez-Gonzalez, Lewis, Burkitt, and Phillips (2011) |
| 00-00-003 | SALVIAS | 4,883 | Brian Enquist | Brad Boyle | |
| 00-00-005 | Tundra Vegetation Plots (TundraPlot) | 577 | Anne D. Bjorkman | Sarah Elmendorf | Elmendorf et al. (2012) |
| 00-RU-002 | Database of Masaryk University's Vegetation Research in Siberia | 1,547 | Milan Chytrý | | Chytrý (2012) |
| AF-00-003 | BIOTA Southern Africa Biodiversity Observatories Vegetation Database | 1,666 | Norbert Jürgens | Gerhard Muche | Muche, Schmiedel, and Jürgens (2012) |
| AF-00-006 | SWEA-Dataveg | 2,704 | Miguel Alvarez | Michael Curran | |
| AF-00-009 | Vegetation Database of the Okavango Basin | 590 | Rasmus Revermann | Manfred Finckh | Revermann et al. (2016) |
| AF-CD-001 | Forest Database of Central Congo Basin | 292 | Elizabeth Kearsley | Hans Verbeeck | Kearsley et al. (2013) |
| AF-ET-001 | Vegetation Database of Ethiopia | 74 | Desalegn Wana | Anke Jentsch | Wana and Beierkuhnlein (2011) |
| AF-MA-001 | Vegetation Database of Southern Morocco | 1,337 | Manfred Finckh | | Finckh (2012) |
| AF-ZA-003* | SynBioSys Fynbos Vegetation Database | 3,810 | John Janssen | | |
| AF-ZW-001* | Vegetation Database of Zimbabwe | 36 | Cyrus Samimi | | Samimi (2003) |
| AS-00-001 | Korean Forest Database | 4,885 | Tomáš Černý | Petr Petřík | Černý et al. (2015) |
| AS-00-003 | Vegetation of Middle Asia | 1,381 | Arkadiusz Nowak | Marcin Nobis | Nowak et al. (2017) |
| AS-00-004 | Rice Field Vegetation Database | 179 | Arkadiusz Nowak | | |

(Continues)

**TABLE 2** (Continued)

| GIVD ID | Database name | # of plots in sPlot 2.1 | Custodian | Deputy custodian | Reference |
|------------|---|-------------------------|-------------------------------------|-------------------|--|
| AS-BD-001 | Tropical Forest Dataset of Bangladesh | 211 | Mohammed A.S. Arfin Khan | Fahmida Sultana | |
| AS-CN-001 | China Forest-Steppe Ecotone Database | 148 | Hongyan Liu | Fengjun Zhao | Liu, Cui, Pott, and Speier (2000) |
| AS-CN-002 | Tibet-PaDeMoS Grazing Transect | 146 | Karsten Wesche | | Wang et al. (2017) |
| AS-CN-003* | Vegetation Database of the BEF China Project | 27 | Helge Bruelheide | | Bruelheide et al. (2011) |
| AS-CN-004* | Vegetation Database of the Northern Mountains in China | 485 | Zhiyao Tang | | |
| AS-CN-005* | Database Steppe Vegetation of Xinjiang | 129 | Kohei Suzuki | | |
| AS-EG-001 | Vegetation Database of Sinai in Egypt | 926 | Mohamed Z. Hatim | | Hatim (2012) |
| AS-ID-001 | Sulawesi Vegetation Database | 24 | Michael Kessler | | |
| AS-IR-001 | Vegetation Database of Iran | 2,335 | Jalil Noroozi | Parastoo Mahdavi | |
| AS-KG-001 | Vegetation Database of South-Western Kyrgyzstan | 452 | Peter Borchardt | Udo Schickhoff | Borchardt and Schickhoff (2012) |
| AS-KZ-001 | Database of Meadow Vegetation in the NW Tian Shan Mountains | 94 | Viktoria Wagner | | Wagner (2009) |
| AS-MN-001 | Southern Gobi Protected Areas Database | 1,516 | Henrik von Wehrden | Karsten Wesche | von Wehrden, Wesche, and Miede (2009) |
| AS-RU-001 | Wetland Vegetation Database of Baikal Siberia (WETBS) | 2,381 | Victor Chepinoga | | Chepinoga (2012) |
| AS-RU-002 | Database of Siberian Vegetation (DSV) | 9,116 | Andrey Korolyuk | Andrei Zverev | |
| AS-RU-004 | Database of the University of Münster - Biodiversity and Ecosystem Research Group's Vegetation Research in Western Siberia and Kazakhstan | 445 | Norbert Hölzel | Wanja Mathar | |
| AS-SA-001* | Vegetation Database of Saudi Arabia | 919 | Mohamed Abd El-Rouf Mousa El-Sheikh | | |
| AS-TJ-001 | Eastern Pamirs | 282 | Kim André Vanselow | | Vanselow (2016) |
| AS-TW-001 | National Vegetation Database of Taiwan | 930 | Ching-Feng Li | Chang-Fu Hsieh | |
| AS-YE-001 | Socotra Vegetation Database | 396 | Michele De Sanctis | Fabio Attorre | De Sanctis and Attorre (2012) |
| AU-AU-002 | TERN AEKOS | 21,261 | Anita Smyth | Ben Sparrow | Turner, Smyth, Walker, and Lowe (2017) |
| AU-NC-001 | New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN) | 201 | Jérôme Munzinger | Philippe Birnbaum | Ibanez et al. (2014) |
| AU-NZ-001 | New Zealand National Vegetation Databank | 1,895 | Susan Wiser | | Wiser, Bellingham, and Burrows (2001) |
| AU-PG-001 | Forest Plots from Papua New Guinea | 63 | Timothy Whitfield | George Weiblen | Whitfield et al. (2014) |

(Continues)

TABLE 2 (Continued)

| GIVD ID | Database name | # of plots in sPlot 2.1 | Custodian | Deputy custodian | Reference |
|------------|---|-------------------------|-----------------------------|-------------------------|--|
| NA-00-002 | Tree Biodiversity Network (BIOTREE-NET) | 1,757 | Luis Cayuela | | Cayuela et al. (2012) |
| NA-CA-003 | Database of Timberline Vegetation in NW North America | 110 | Viktoria Wagner | Toby Spribille | Wagner, Spribille, Abrahamczyk, and Bergmeier (2014) |
| NA-CA-004 | Understory of Sugar Maple Dominated Stands in Quebec and Ontario (Canada) | 156 | Isabelle Aubin | | Aubin, Gachet, Messier, and Bouchard (2007) |
| NA-CA-005* | Boreal Forest of Canada | 89 | Yves Bergeron | Louis De Grandpré | |
| NA-GL-001 | Vegetation Database of Greenland | 664 | Birgit Jedrzejek | Fred J.A. Daniëls | Sieg, Drees, and Daniëls (2006) |
| NA-US-002 | VegBank | 67,352 | Robert K. Peet | Michael T. Lee | Peet et al. (2012) |
| NA-US-006 | Carolina Vegetation Survey Database | 17,221 | Robert K. Peet | Michael T. Lee | Peet et al. (2012) |
| NA-US-014 | Alaska-Arctic Vegetation Archive | 1,363 | Donald A. Walker | Amy Breen | Walker et al. (2016) |
| SA-00-002 | VegPáramo | 2,643 | Gwendolyn Peyre | Xavier Font | Peyre et al. (2015) |
| SA-AR-002 | Vegetation Database of Central Argentina | 218 | Marcelo R. Cabido | Alicia Acosta | |
| SA-BO-003 | Bolivia Forest Plots | 75 | Michael Kessler | Sebastian Herzog | |
| SA-BR-002 | Forest Inventory, State of Santa Catarina, Brazil (IFFSC Project) | 1,669 | Alexander Christian Vibrans | André Luis de Gasper | Vibrans, Sevegnani, Lingner, de Gasper, and Sabbagh (2010) |
| SA-BR-003 | Grasslands of Rio Grande do Sul, Brazil | 320 | Eduardo Vélez-Martin | Valério De Patta Pillar | |
| SA-BR-004 | Grassland Database of Campos Sulinos | 161 | Gerhard E. Overbeck | Valério De Patta Pillar | |
| SA-CL-002 | SSAForests_Plots_db | 261 | Alvaro G. Gutierrez | | |
| SA-CL-003* | Chilean Park Transects - Fondecyt 1040528 | 165 | Aníbal Pauchard | Alicia Marticorena | Pauchard, Fuentes, Jiménez, Bustamante, and Marticorena (2013) |
| SA-EC-001 | Ecuador Forest Plot Database | 172 | Jürgen Homeier | | |

Note. GIVD ID refers to the ID in the Global Index of Vegetation-Plot Databases (<http://www.givd.info>), which manages the metadata for sPlot and provides updated online descriptions of these databases; * after the GIVD ID indicates that the respective database description is currently not visible on the GIVD website. Datasets contributed in harmonized format from a continental data aggregator ("collective database" according to the sPlot Rules) are listed under its name. Further references, attributions and disclaimers for particular datasets are found Appendix S1.

>25%. Similarly, we defined non-forests by calculating the cover of all taxa that were not defined as trees or shrubs (also taken from the TRY plant growth form information) and that were not taller than 2 m, using the TRY data on mean plant height. In total, 21,888 taxa belonged to this category. We defined all plots as non-forests if the sum of relative cover of these low-stature, non-tree and non-shrub taxa was >90%. As we did not have the growth form and height information for all taxa, a fraction of about 25% of the plots remained unassigned (i.e., neither forest, nor non-forest). In addition, more detailed classifications of plots into physiognomic formations (Table S3.2 in Appendix S3) and naturalness (Table S3.3 in Appendix S3) were derived from various types of plot-level or database-level information provided by the sources and stored in five separate fields (see Table S2.1 in Appendix S2).

2.4 | Phylogenetic information

We developed a workflow to generate a phylogeny of the vascular plant species in sPlot, using the phylogeny of Zanne et al. (2014), updated by Qian and Jin (2016). Species present in sPlot but missing from this phylogeny were added next to a randomly selected congener (see also Maitner et al., 2018). This approach has been demonstrated to introduce less bias into subsequent analyses than adding missing species as polytomies to the respective genera (Davies, Kraft, Salamin, & Wolkovich, 2012). We only added species based on taxonomic information on the genus level, thus not making use of family affiliation. Because of the absence of congeners in the reference phylogeny, 7,147 species could not be added (11.7% of all resolved taxa in sPlot and TRY). This resulted in a phylogeny

with 54,067 resolved taxon names from 61,214 standardized taxa in the combined list of sPlot and TRY. The tree was finally pruned to the vascular plant taxa of the current sPlot version 2.1, resulting in a phylogenetic tree for 53,489 out of the 58,066 taxa in sPlot. Of these 53,489 names, 16,026 are also found among the 31,389 taxa in the phylogenetic tree of Qian and Jin (2016), i.e., 51.1%. The full procedure and the R code are available in Purschke (2017b).

2.5 | Associated environmental plot information

To complement the plot data, we harmonized geographical coordinates (in decimal degrees), elevation (m above sea level), aspect (degrees) and slope (degrees) as provided by the contributing databases. All other variables were too sparsely and too inconsistently sampled across databases to be combined in the global set, but were retained in the original data sources and can be retrieved for particular purposes.

We used the geographic coordinates to create a geodatabase in ArcGIS 14.1 (ESRI, Redlands, CA) to link sPlot 2.1 to these climate and soil data. We retrieved data for all the 19 bioclimatic variables provided by CHELSA v1.1 (Karger et al., 2017) by averaging climatic data from the period 1979–2013 at 30 arc seconds (about 1 km in grid cells near to the equator). These variables are the same as the ones used in WorldClim (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), but calculated with a downscaling approach based on estimates of the ERA-Interim climatic reanalysis (Dee et al., 2011). While the CHELSA climatological data have a similar accuracy as other products for temperature, they are more precise for precipitation patterns (Karger et al., 2017). We also

calculated growing degree days for 1°C (GDD1) and 5°C (GDD5), according to Synes and Osborne (2011) and based on CHELSA data, and included the index of aridity and potential evapotranspiration extracted from the CGIAR-CSI website (www.cgiar-csi.org). In addition, we extracted seven soil variables from the SOILGRIDS project (https://soilgrids.org/; licensed by ISRIC – World Soil Information), downloaded at 250-m resolution and then converted to the same 30-arc second grid format of CHELSA. To explore the distribution of sPlot data in the global environmental space, we subjected all 30 climate and soil variables of the global terrestrial surface rasterized on a 2.5 arc-minute grid resolution to a principal component analysis (PCA) on standardized and centered data. We subsequently created a grid of 100 cells \times 100 cells within the bi-dimensional environmental space defined by the first two PCA axes (PC1 and PC2) and counted the number of terrestrial cells per environmental grid cell of the PC1-PC2 space. Then, we counted the number of plots in sPlot in the same PCA grid (Figure 2).

We linked all vegetation plots to two global biome classifications. We used the World Wildlife Fund (WWF) spatial information on terrestrial ecoregions (Olson et al., 2001) to assign plots to one of the 867 ecoregions, 14 biomes and eight biogeographic realms. The WWF approach is based on a bottom-up expert system using various regional biodiversity sources to define ecoregions, which in turn are grouped into realms and biomes (Olson et al., 2001). In addition, we created a shapefile for the ecozones defined by Schultz (2005) to represent major biomes in response to global climatic variation. Since these zones are climatically heterogeneous in mountain regions, we differentiated an additional “alpine” biome for mountain areas above the lower mountain thermal

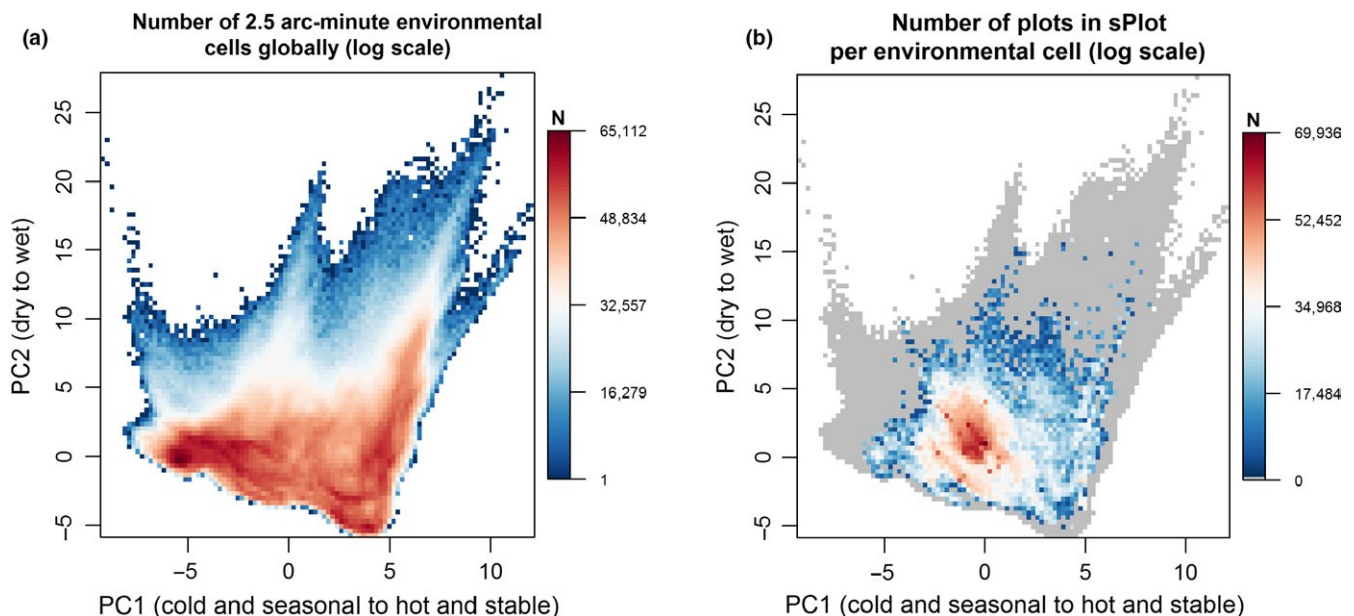


FIGURE 2 Distribution of vegetation plots from sPlot 2.1 in the global environmental space. Comparison of the distribution of all terrestrial 2.5 arc-minute cells (a) and plots in sPlot 2.1 (b) in the principal component analysis (PCA) space defined on 30 environmental (climate and soil) variables. The PCA space was divided into a 100 \times 100 regular grid. For each element of this grid, the graphs show the number of 2.5 arc-minute cells (a) and plots (b), respectively. Colors refer to the logarithm of number of plots, with the legend showing untransformed number of plots. The first and second PCA axis explained 48.6% and 27.3% of the total variance

belt, as defined in the classification of world mountain regions by Körner et al. (2017). This resulted in a distinction of 10 major biomes (Figure S4.5 in Appendix S4), whose shapefile is freely available (Appendix S5).

2.6 | Trait information

To broaden the potential applications of the global vegetation database in functional contexts, we linked sPlot to TRY. We accessed plant trait data from TRY version 3.0 on August 10, 2016, and included 18 traits that describe the leaf, wood and seed economics spectra (Westoby, 1998; Reich, 2014; Table S6.4 in Appendix S6), and are known to affect different key ecosystem processes and to respond to macroclimatic drivers. These traits were represented across all species in the TRY database by at least 1,000 trait records. We excluded trait records from manipulative experiments and outliers (Kattge et al., 2011), which resulted in a matrix with 632,938 individual plant records on 52,032 taxa in TRY, having data records for an average of 3.08 of the 18 selected traits. On average, each trait has been measured at least once in 17.1% of all taxa. In order to attain data for these 18 traits for all species with at least one trait value in TRY, we employed hierarchical Bayesian modeling, using the R package 'BHPMF' (Fazayeli, Banerjee, Kattge, Schrod, & Reich, 2017; Schrod et al., 2015), to fill a gap in the matrix of individual plant records in TRY. Gap filling allows obtaining trait values for a species on which this trait has not been measured, but for which other traits are available. To assess gap-filling quality, we used the probability density distributions provided by BHPMF for each imputation and removed highly uncertain imputations with a coefficient of variation >1. We then log_e-transformed all gap-filled trait values and averaged each trait by taxon. For taxa recorded at genus level only, we calculated genus means, resulting in a full trait matrix for 26,632 out of the 54,519 taxa in sPlot (45.9%), with 6, 1,510 and 25,116 taxa at the family, genus and species level, respectively. These species covered 88.7% of all species-by-plot combinations.

For every trait j and plot k , we calculated the community-weighted mean (CWM) and the community-weighted variance (CWV) for each of the 18 traits in a plot (Enquist et al., 2015):

$$CWM_{j,k} = \sum_i^{n_k} p_{i,k} t_{i,j}$$

$$CWV_{j,k} = \sum_i^{n_k} p_{i,k} (t_{i,j} - CWM_{j,k})^2$$

where n_k is the number of species with trait information in plot k , $p_{i,k}$ is the relative abundance of species i in plot k calculated as the species' fraction in cover or abundance of total cover or abundance, and $t_{i,j}$ is the mean value of species i for trait j . CWMs and CWVs were calculated for 18 traits in 1,117,369 and 1,099,463 plots, respectively, the second being a smaller number as at least two taxa were needed for CWV calculation.

3 | CONTENT OF SPLOT 2.1

3.1 | Plot community data

sPlot 2.1 contains 1,121,244 vegetation plots from 160 countries and from all continents (Figure 3). The global coverage is biased towards Europe, North America and Australia, reflecting unequal sampling effort across the globe (Table 1). At the ecoregion level, major gaps occur in the wet tropics of South America and Asia, as well as in subtropical deserts worldwide and in the North American taiga. Although the plots are highly clustered geographically, their coverage in the environmental space is much more representative: the highest concentration of plots is found in environments that are most abundant globally (Figure 2), while they are lacking in the very moist parts of the environmental space, which are also spatially rare, and in the very cold parts, which are sparsely vegetated.

In most cases (98.4%), plot records in sPlot include full species lists of vascular plants, while 1.6% had only wood species above a certain diameter or only the most dominant species recorded. Terricolous bryophytes and lichens were additionally identified in 14% and 7% of plots, respectively (Table S2.1 in Appendix S2). Forest and non-forest plots comprise 330,873 (29.7%) and 513,035 (46.0%) of all plots in sPlot, respectively. In most cases, species abundance was estimated using different variants of the Braun-Blanquet cover-abundance scale (66%), followed by percentage cover (15%) and 55 other numeric or ordinal scales. The temporal extent of the data spans from 1885 to 2015, but >94% of vegetation plots were recorded later than 1960 (Figure S2.1 in Appendix S2). Almost all plots are georeferenced (1,120,686) and the majority of plots have location uncertainty of 10 m or less (Figure S2.2 in Appendix S2).

Vascular plant richness per plot ranges from 1 to 723 species (median = 17 species). The most frequent richness class is between 20 and 25 species (Figure S2.3 in Appendix S2). Plot size is reported in 65.4% of plots, ranging from <1 m² to 25 ha, with a median of 36 m². While forest plots have plot sizes ≥100 m², and in most cases ≤1,000 m², non-forest plots range between 5 and 100 m² (Figure S2.4 in Appendix S2). When using these size ranges, forest plots tend to be richer in species (Figure 4a). The fact that the gradient in richness found in our plots was at least one order of magnitude stronger than differences that could be expected by the differences in plot size prompted us to produce the first global maps of plot-scale species richness, separately for forests and non-forests (Figure 4a). While plots with complete vascular species composition are largely lacking from the wet tropics, for the remaining biomes the plot-scale richness data do not show the typical latitudinal richness gradient in either formation. Particularly species-rich forests are found in the wet subtropics (such as SE United States, Taiwan and the East coast of Australia) as well as in some mountainous regions of the nemoral and steppic biomes of Eurasia. Likewise, non-forest communities have a particularly high mean vascular plant species in mountainous regions of the nemoral and steppic biomes of Eurasia.

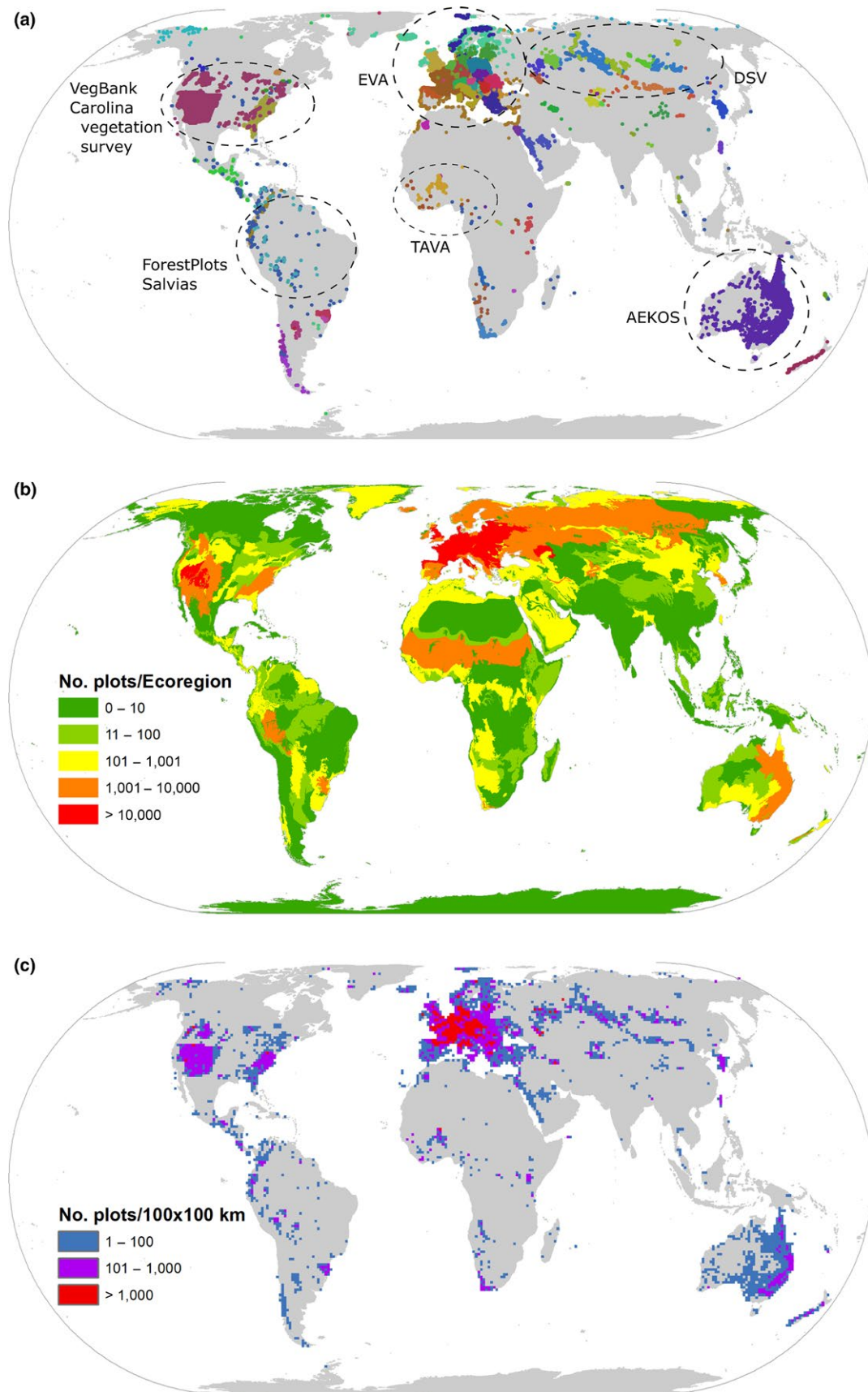


FIGURE 3 Global coverage of sPlot 2.1. (a) Contributing databases identified by different colours with indication of the two data aggregators (EVA, TAVA) and a few particularly large individual databases; (b) available plot numbers per WWF Ecoregion; and (c) available plot density in grid cells of 100 km × 100 km

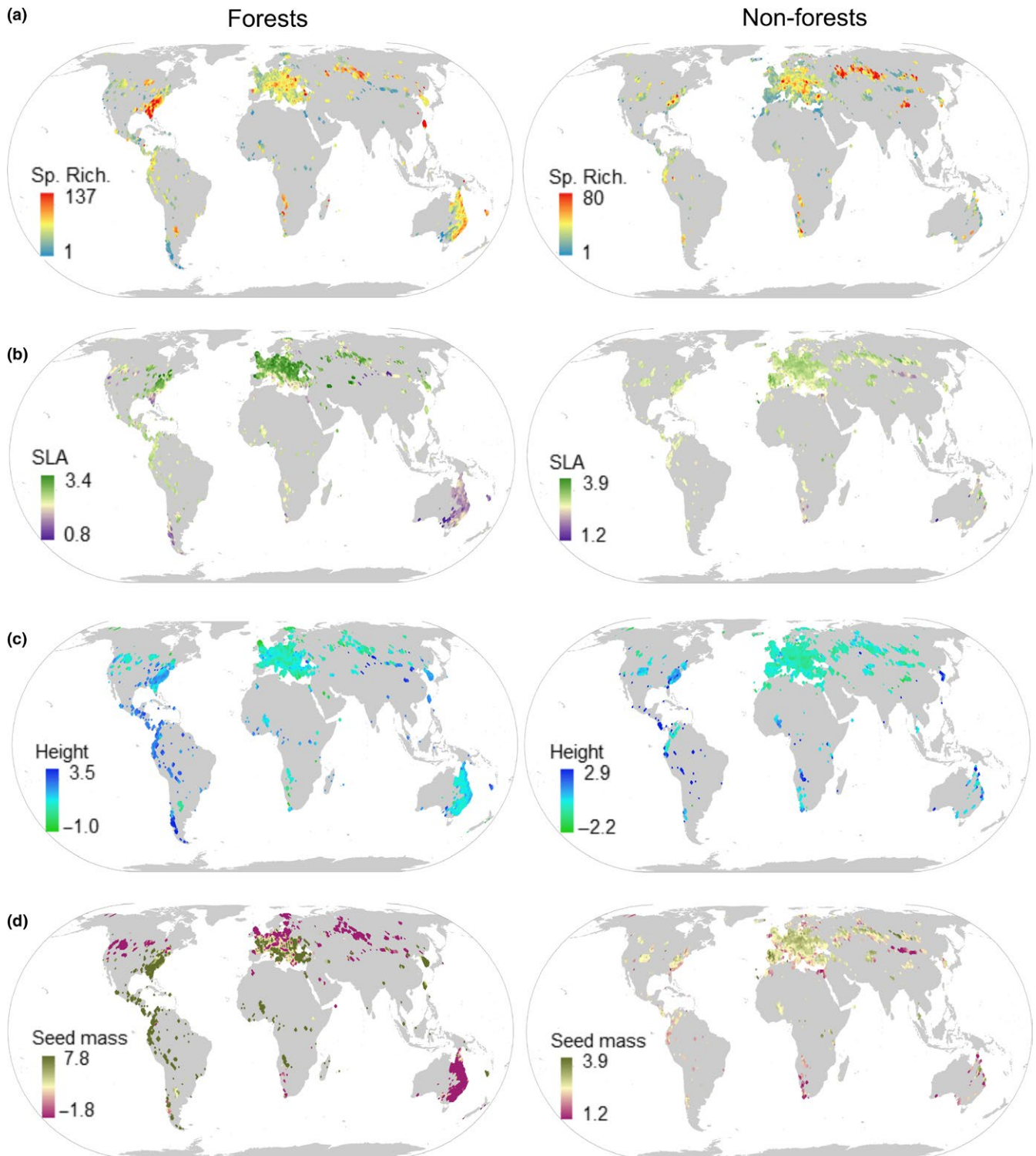


FIGURE 4 Examples of global community-level patterns that can be derived from (a) sPlot alone and (b–d) sPlot combined with TRY, here shown as raw data averaged by 1-degree grid cells. There are only a very few cells (142 out of 2633) comprising only a single plot. For the maps, only plots with full vascular species composition and spatial accuracy <5 km were used. They are based on 148,474 and 218,051 plots for forests and non-forests, respectively. Note that these maps are not corrected for biases caused by the facts that not all community types were recorded in all grid cells and that plot sizes as well as the fraction of species with available trait data varied spatially. Maps show patterns of (a) fine-grain alpha diversity, expressed as vascular plant species richness (only plots with plot sizes of 100–1000 m² for forests and 5–100 m² for non-forests); (b) community-weighted means (CWMs) for log_e-transformed trait values of specific leaf area (SLA, m²/kg); (c) plant height (m); and (d) seed mass (mg)

3.2 | Phylogenetic information

The phylogenetic tree for sPlot was produced from 53,489 vascular plant names contained in the database, comprising 5518 genera (Appendix S7). Moderately to highly frequent species in sPlot 2.1 are equally distributed across the phylogeny (corresponding to yellowish to reddish colors for low and high peaks, respectively, in Figure S7.6 in Appendix S7). Coverage of species included in the phylogeny ranges from 89% of species that occur only once in all plots to 100% of species with a frequency >10,000 plots (Figure S7.7 in Appendix S7).

3.3 | Functional information

The proportion of species with trait information increases with the species' frequency in plots. Gap-filled trait information is available for 77.2% and 96.2% for taxa that occurred in more than 100 and 1,000 plots, respectively. Trait coverage is similar across biomes (Figure S8.8 in Appendix S8). Across all biomes, the proportion of species for which gap-filled trait data are available increases with the species' frequency across plots. Compared to gap-filled data, trait coverage for the original trait data is considerably lower, being highest for height, seed mass, leaf area and specific leaf area (SLA, Figure S8.9 in Appendix S8).

The high representation of the 18 traits in the gap-filled trait data and the high degree of trait coverage for frequent species across all biomes (>75%) made us confident to produce the first maps of global patterns of community-weighted means (CWMs) (Figure 4b–d). The maps show the main trait dimensions of SLA, height and seed mass, separately for forests and non-forests, for those regions of the world that are already sufficiently covered by sPlot data. Accordingly, CWMs of SLA are quite similar for forest and non-forest plots, being highest in western North America and Europe and lowest in eastern North America, East and South Australia (Figure 4b). Non-forest vegetation shows lowest CWMs of SLA in the desert regions of the Namib and Sinai. Forests with highest CWMs of canopy height are found along the western and eastern coast of North America, some regions in Europe, East Asia and southern Australia (Figure 4c). These areas only partly coincide with those of highest seed masses for forests, while seed mass in non-forests is highest in the eastern Mediterranean Basin and in Central Asia (Figure 4d). The corresponding patterns for CWV are shown in Figure S9.10 in Appendix S9.

4 | DATA USAGE

The sPlot database (the vegetation-plot data, including the environmental information for each plot and the species phylogeny) is released in fixed versions to allow reproducibility of results, but also due to the enormous effort needed for data integration and harmonization and for updating the phylogeny. By delivering few fixed versions while keeping older versions available, the sPlot consortium

ensures that the same data can be used in parallel projects and that the data underlying a specific study remain accessible in the future, thus allowing re-analysis. Each new version will be matched to the current TRY database.

Data access to sPlot is regulated by the Governance and Data Property Rules (www.idiv.de/sPlot) to ensure a fair balance between the interests of data contributors and data analysts. In brief, the sPlot Rules state that: (a) all contributing vegetation-plot databases become members of the sPlot consortium, represented by their custodian and deputy custodian; (b) vegetation-plot data contributed to sPlot remain the property of the data contributors and can be withdrawn at any time except for approved projects; (c) other scientists (e.g., data managers or participants of the sPlot workshops) with particular responsibilities may also be appointed as personal members to the sPlot consortium; (d) sPlot data can be requested for projects that involve at least one member of the sPlot consortium; (e) whenever a project has been proposed, all sPlot consortium members will be informed and can declare their interest in becoming co-authors of manuscripts resulting from this project and then becoming actively involved in data evaluation and writing; and (f) if also the matched gap-filled or original trait data from TRY are requested for a project, likewise members from the TRY consortium can opt-in as co-authors. The sPlot database is, therefore, available according to a 'give-and-receive' system. Moreover, the data are available to any researcher by establishing a collaboration that includes and is supported by at least one sPlot consortium member.

The sPlot consortium is governed by a Steering Committee elected by all consortium members for two-year, renewable terms. Project proposals can be submitted to the Steering Committee, which ensures that the sPlot Rules are followed and redundant work between overlapping projects is avoided. The lists of databases, sPlot consortium members and the Steering Committee members are updated regularly on the sPlot website, as are the sPlot Rules and the list of approved projects.

5 | EXPECTED IMPACT AND LIMITATIONS

The main aim of the sPlot database is to catalyze a collaborative network for understanding global diversity patterns of plant communities in space and time. sPlot provides a unique, integrated global repository of data that would otherwise be fragmented in unconnected and structurally inconsistent databases at regional, national or continental levels. Together with the provision of harmonized phylogenetic, functional and environmental information, sPlot allows, for the first time, global analyses of plant community data. Compared to approaches using data aggregated from species occurrences in grid cells, sPlot will significantly advance ecological analyses and future interdisciplinary research in at least four different ways.

1. Using sPlot, one can predict the species that can co-exist in a community and also the frequencies of their co-occurrence

(Breitschwerdt, Jandt, & Bruehlheide, 2015) or niche overlap (Broennimann et al., 2012). In addition, emerging tools such as Markov networks can be used to infer strengths of interspecific interactions (Harris, 2016). When investigating community assembly rules, the same information can be used to derive species pools for specific vegetation types (de Bello et al., 2016; Karger et al., 2016; Lewis, Szava-Kovats, & Pärtel, 2016). Moreover, the co-occurrence data from sPlot can be used to address fundamental patterns and drivers of plant invasions better than information on large geographic entities (e.g., van Kleunen et al., 2015) alone could.

2. sPlot data can be aggregated across all types of plots, by grid cells, ecoregions, environment, or even vegetation type or formation. Furthermore, replicated plots within grid cells, ecoregions, or any other subdivision of environmental conditions or vegetation types allow users to derive measures of compositional differences between plant communities within grid cells (= beta diversity; Table 1). Thus, the community data are an important complement to regional-scale species occurrence data (e.g., Enquist et al., 2016; Kreft & Jetz, 2007).
3. sPlot data provide information on the proportion of species in a community (in terms of cover, basal area, frequency). When combined with functional trait information, relative abundance of species allows calculation of community abundance-weighted mean trait values (Bruehlheide et al., 2018). Information on the relative contribution of species to a community-aggregated trait value is particularly necessary when traits are used as proxies for vegetation functions and processes, allowing to test, among other things, the mass ratio hypothesis (Garnier et al., 2004; Grime, 1998) and to assess the roles of divergent traits (Díaz et al., 2007; Kröber et al., 2015).
4. Plant species within plots can be linked to traits that predict interactions with organisms from other trophic groups, both below-ground (mycorrhizae, soil decomposers) and above-ground (herbivores and pollinators). This will allow linking vegetation plot information to ecosystem processes and services such as pest control, pollination and nutrient cycling (e.g., de Bello et al., 2010).

Despite the large amount of available data and its potential suitability for global research, a number of limitations must be considered by future users of sPlot, such as (a) biases towards certain regions and communities, (b) near-complete lack of plots with complete vascular plant species composition for certain regions (e.g., the wet tropics), (c) identification or sampling errors by the surveyors and incomplete records because the detection of some species may be precluded in certain seasons by their phenology, (d) taxonomic uncertainty, particularly in the tropics, (e) strongly varying plot sizes employed in different studies and regions, (f) lack of trait measures at the plot level. For example, patterns of diversity components are typically affected by grain size. This means that using sPlot data for such studies either requires filtering for plots with identical or at least similar size or accounting for the plot-size effects in the statistical model. In addition, analyses of functional diversity with sPlot data are limited by the absence of

trait data for a (small) portion of the species and by the lack of plot-specific trait measures. Furthermore, the non-random and geographically and ecologically very unequal distribution of the plots contained in sPlot call for stratified resampling to balance records of different environments (e.g., stratified by climate, Figure 2) or physiognomic formations (Figure 4). Users of sPlot need to be aware of these and other limitations and to correct potential biases for their specific research question.

6 | CONCLUSION

sPlot is a unique global database of plant community records sampled with relatively similar methods widely used in vegetation ecology. The integration of co-occurrence data into a unified database that can be directly linked to environmental, functional and phylogenetic information, makes sPlot an unprecedented and essential tool for analyzing global plant diversity, the structure of plant communities and the co-occurrence of plant species. The compatibility of this consolidated database with other global databases, e.g., via a joint taxonomic backbone with TRY and the Global Naturalized Alien Flora (GloNAF; van Kleunen et al., 2015) (via taxon names), or via standardized geo-reference with databases of environmental information such as CHELSA, WorldClim or SoilGrids (Bruehlheide et al., 2018), facilitates data integration and creates new research opportunities. The adaptive management of the database employed by the sPlot consortium allows regular incorporation of new data, resulting in a dynamic platform for storing and analyzing the most comprehensive compilation of plant community data worldwide.

ACKNOWLEDGEMENTS

We are grateful to thousands of vegetation scientists who sampled vegetation plots in the field or digitized them into regional, national or international databases. We also appreciate the support of the German Research Foundation for funding sPlot as one of the iDiv (DFG FZT 118) research platforms, and the organization of three workshops through the sDiv calls. We acknowledge this support with naming the database “sPlot”, where the “s” refers to the sDiv synthesis workshops. The study was supported by the TRY initiative on plant traits (<http://www.try-db.org>). For all further acknowledgements see Appendix S10. We thank Meelis Pärtel for his very fast and constructive feedback on an earlier version of this manuscript.

AUTHOR CONTRIBUTIONS

H.Bru. had the original idea and led the consortium from the start, while O.Pu. and J.D. coordinated the sPlot workshops. J.D., S.M.H. and U.J. compiled the databases to be included in sPlot. J.D. and later B.J.-A. and F.M.S. coordinated the network and the database. O.P. prepared the taxonomic and phylogenetic data. S.M.H. programmed the Turboveg software. B.Sa., F.J., H.Bru., J.D., J.K., M.Ch., and V.D.P.



organized the network in the Steering Committee. B.J.-A. and H.Bru. led the writing together with J.D. and input from S.M.H., O.Pu., M.Ch., F.J., J.K., V.D.P., B.Sa., I.Au., I.B., R.K.P., R.F., S.H., U.J., J.L., G.P., F.M.S., M.S., F.S. and M.W. The rest of authors (ordered alphabetically) contributed the plot and trait data. All authors agreed with the final manuscript.

DATA ACCESSIBILITY

The data contained in sPlot (the vegetation-plot data complemented by species phylogeny and environmental information) are available on request, through contacting any of the consortium members for submitting a paper proposal. The proposals should follow the Governance and Data Property Rules of the sPlot Working Group, which are available on the sPlot website (www.idiv.de/sPlot). After acceptance, the respective data will be provided. In addition to the plot data, CWMs and CWVs of 18 plant traits are available for every plot.

ORCID

Helge Bruelheide <https://orcid.org/0000-0003-3135-0356>
 Jürgen Dengler <https://orcid.org/0000-0003-3221-660X>
 Borja Jiménez-Alfaro <https://orcid.org/0000-0001-6601-9597>
 Oliver Purschke <https://orcid.org/0000-0003-0444-0882>
 Milan Chytrý <https://orcid.org/0000-0002-8122-3075>
 Valério D. Pillar <https://orcid.org/0000-0001-6408-2891>
 Jens Kattge <https://orcid.org/0000-0002-1022-8469>
 Idoia Biurrun <https://orcid.org/0000-0002-1454-0433>
 Richard Field <https://orcid.org/0000-0003-2613-2688>
 Jonathan Lenoir <https://orcid.org/0000-0003-0638-9582>
 Robert K. Peet <https://orcid.org/0000-0003-2823-6587>
 Francesco Maria Sabatini <https://orcid.org/0000-0002-7202-7697>
 Marco Schmidt <https://orcid.org/0000-0001-6087-6117>
 Franziska Schrodtt <https://orcid.org/0000-0001-9053-8872>
 Emiliano Agrillo <https://orcid.org/0000-0003-2346-8346>
 Miguel Alvarez <https://orcid.org/0000-0003-1500-1834>
 Pierangela Angelini <https://orcid.org/0000-0002-5321-9757>
 Mohammed A. S. Arfin Khan <https://orcid.org/0000-0001-6275-7023>
 Fabio Attorre <https://orcid.org/0000-0002-7744-2195>
 Michael Beckmann <https://orcid.org/0000-0002-5678-265X>
 Yves Bergeron <https://orcid.org/0000-0003-3707-3687>
 Erwin Bergmeier <https://orcid.org/0000-0002-6118-4611>
 Zoltán Botta-Dukát <https://orcid.org/0000-0002-9544-3474>
 Chaeho Byun <https://orcid.org/0000-0003-3209-3275>
 Laura Casella <https://orcid.org/0000-0003-2550-3010>

Luis Cayuela <https://orcid.org/0000-0003-3562-2662>
 Tomáš Černý <https://orcid.org/0000-0003-2637-808X>
 Victor Chepinoga <https://orcid.org/0000-0003-3809-7453>
 János Csiky <https://orcid.org/0000-0002-7920-5070>
 Els De Bie <https://orcid.org/0000-0001-7679-743X>
 Michele De Sanctis <https://orcid.org/0000-0002-7280-6199>
 Jaime Fagúndez <https://orcid.org/0000-0001-6605-7278>
 Xavier Font <https://orcid.org/0000-0002-7253-8905>
 Estelle Forey <https://orcid.org/0000-0001-6082-3023>
 André Luis Gasper <https://orcid.org/0000-0002-1940-9581>
 Alvaro G. Gutierrez <https://orcid.org/0000-0001-8928-3198>
 Tianhua He <https://orcid.org/0000-0002-0924-3637>
 Pedro Higuchi <https://orcid.org/0000-0002-3855-555X>
 Norbert Hölzel <https://orcid.org/0000-0002-6367-3400>
 Steven Jansen <https://orcid.org/0000-0002-4476-5334>
 Martin Jiroušek <https://orcid.org/0000-0002-4293-478X>
 Norbert Jürgens <https://orcid.org/0000-0003-3211-0549>
 Ali Kavğacı <https://orcid.org/0000-0002-4549-3668>
 Elizabeth Kearsley <https://orcid.org/0000-0003-0046-3606>
 Michael Kessler <https://orcid.org/0000-0003-4612-9937>
 Ingolf Kühn <https://orcid.org/0000-0003-1691-8249>
 Flavia Landucci <https://orcid.org/0000-0002-6848-0384>
 Ching-Feng Li <https://orcid.org/0000-0003-0744-490X>
 Peter Manning <https://orcid.org/0000-0002-7940-2023>
 Corrado Marcenò <https://orcid.org/0000-0003-4361-5200>
 Maurizio Mencuccini <https://orcid.org/0000-0003-0840-1477>
 Vanessa Minden <https://orcid.org/0000-0002-4933-5931>
 Jesper Erenskjold Moeslund <https://orcid.org/0000-0001-8591-7149>
 Marco Moretti <https://orcid.org/0000-0002-5845-3198>
 Jérôme Munzinger <https://orcid.org/0000-0001-5300-2702>
 Ülo Niinemets <https://orcid.org/0000-0002-3078-2192>
 Arkadiusz Nowak <https://orcid.org/0000-0001-8638-0208>
 Gerhard E. Overbeck <https://orcid.org/0000-0002-8716-5136>
 Wim A. Ozinga <https://orcid.org/0000-0002-6369-7859>
 Hristo Pedashenko <https://orcid.org/0000-0002-6743-0625>
 Josep Peñuelas <https://orcid.org/0000-0002-7215-0150>
 Aaron Pérez-Haase <https://orcid.org/0000-0002-5974-7374>
 Petr Petřík <https://orcid.org/0000-0001-8518-6737>
 Oliver L. Phillips <https://orcid.org/0000-0002-8993-6168>
 Cyrus Samimi <https://orcid.org/0000-0001-7001-7893>
 Jozef Šibík <https://orcid.org/0000-0002-5949-862X>
 Željko Škvorc <https://orcid.org/0000-0002-3052-699X>

Jens-Christian Svenning  <https://orcid.org/0000-0002-3415-0862>

Grzegorz Swacha  <https://orcid.org/0000-0002-6380-2954>

Emin Ugurlu  <https://orcid.org/0000-0003-0824-1426>

Eduardo Vélez-Martin  <https://orcid.org/0000-0001-8028-8953>

Roberto Venanzoni  <https://orcid.org/0000-0002-7768-0468>

Risto Virtanen  <https://orcid.org/0000-0002-8295-8217>

Evan Weiher  <https://orcid.org/0000-0002-5375-9964>

Timothy Whitfeld  <https://orcid.org/0000-0003-1850-6432>

Susan Wiser  <https://orcid.org/0000-0002-8938-8181>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Additional references, attributions and disclaimers for datasets included in sPlot 2.1

Appendix S2 Data associated to the vegetation plot records stored in sPlot 2.1

Appendix S3 Details on the workflow for setting up plot definitions in sPlot 2.1

Appendix S4 Biome classification created for sPlot 2.1

Appendix S5 Zip file of the biome classification of Appendix S4 containing the shapefile (Geospatial vector data for geographic

information system (GIS) software) and accompanying accessory files (database, projection etc.)

Appendix S6 Trait information in sPlot 2.1

Appendix S7 Phylogenetic information in sPlot 2.1

Appendix S8 Gap-filled trait information

Appendix S9 Global patterns of community-weighted variances

Appendix S10 Detailed acknowledgements

How to cite this article: Bruelheide H, Dengler J, Jiménez-Alfaro B, et al. sPlot – A new tool for global vegetation analyses. *J Veg Sci.* 2019;30:161–186. <https://doi.org/10.1111/jvs.12710>